PLANT SYSTEMATICS AND CONSERVATION: SCIENCE AND SOCIETY

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ABSTRACT

Systematics is the preeminent science of biodiversity. Differences among species, and among natural phylogenetic groupings of species, represent the major legacy of biological diversification on earth. Pressures of development are causing an alarming increase in the rate of species extinction; intelligent decisions concerning the use or preservation of any species hinge on the existence of a fundamental understanding of species boundaries, species origins, and species relationships, making a renaissance in systematics especially timely. Newly developed methods for data gathering and analysis of phylogenetic relationships (i.e., the genealogy of species) position us on the threshold of a deep understanding of the history of the biological world, but too few systematists are being educated to meet the increased demands for phylogenetic research and its integration into conservation biology. We must break down the widely perceived (but false) barrier between "academic" phylogenetic systematic studies and "applied" studies of floristics and plant conservation; species preservation efforts that are carefully focused and justified by phylogenetic criteria will receive much greater public support. Because of its unusual combination of attributes, with large herbaria and botanical garden as well as a number of supporting laboratories located within a major research university, the University of California at Berkeley can make a unique contribution within California (and indeed the western United States) to this process of integration of systematics and conservation through efforts in both research and education.

Systematics is *the* science of biodiversity. To be sure, other biological, chemical, and physical disciplines provide supporting data. However, systematics (which is the study of phylogenetic relationships among species and among natural groupings of species, and the development of classifications based on those relationships) is most directly concerned with the legacy of biological diversification on earth. Systematics specifically informs decisions regarding the use and preservation of genetic diversity of cultivated plants, domesticated animals, wild progenitors of these species, and the closest relatives of these wild progenitors. In addition to such taxa of obvious value to humanity, intelligent decisions concerning the use or preservation of *any* species hinge on the existence of a fundamental understanding of species boundaries, species origins, and species relationships.

Pressures of development are causing an alarming increase in the

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rate of species extinction. Loss of biological diversity is a disaster, both from the commonly cited economic standpoint (the potential extinction of many organisms useful for food, medicine, or technology) but also from a broader intellectual standpoint—all living things are *literally* our relatives, and one of our biggest and potentially most satisfying intellectual challenges is to know their (and thus our) genealogy. Fortunately given the timing of the current crisis, newly developed methods for data gathering and analysis of phylogenetic relationships (i.e., the genealogy of species) position us on the threshold of a deep understanding of the history of the biological world. Just in the nick of time, we are moving towards improved classifications of organisms and improved means of applying this knowledge to their conservation.

In this paper I will address each of the three subtitles to the symposium: research, education, and conservation, in both a general and a specific context (i.e., how can we at the Jepson Herbarium and the University of California address these concerns?). Each of these issues revolves around *the* fundamental task of systematics: *phylogeny reconstruction.* Since this connection is not widely realized by either the general public or botanical specialists, I need to begin by explaining the principles of modern Hennigian phylogenetics and then explore its role as a basis for setting conservation priorities.

Phylogenetic Systematics

The field of systematics underwent a conceptual upheaval in the 1970's and 1980's—for an insightful history, see the masterful book by David Hull (1988). Many issues were at stake in the "systematics wars," foremost of which was the nature of taxa. Are they just convenient groupings of organisms with similar features, or are they lineages, marked by homologies? The consensus view these days among most systematists is that taxa are the latter, but why? Why is phylogenetic integrity necessary for species and other taxa? Taxa could, of course, be whatever we want, since the whole nomenclature system is a human construct (i.e., the naming system *is* a series of legislated conventions, even though the units being named may well be real). Many kinds of non-phylogenetic biological groupings have been proposed that are unquestionably useful for special purposes (e.g., "predators," "rain forests," "succulent plants," "bacteria"). However, phylogenetic systematists (cladists, the great majority of systematists now) have settled on phylogeny as the best criterion for general purpose classification. Understanding why this choice was made requires some background.

Like other cutting-edge areas of biology, phylogenetic systematics is loaded with terminology and quantitative methods, yet the basic principle is quite simple (for further information see Wiley 1981;

Funk and Brooks 1990; Brooks and McLennan 1991; Mishler and De Luna 1991; Mishler 1994). The fundamental idea is known as the *Hennig Principle,* and is as elegant and fundamental in its way as was Darwin's principle of natural selection. It is indeed simple, yet profound in its implications. It is based on the idea of *homology,* one of the most important concepts in systematics, but also one of the most controversial. What does it mean to say that two organisms share the same characteristic? The modern concept is based on evidence for historical continuity of information (Van Valen 1982; Roth 1988); homology would then be defined as a feature shared by two organisms because of descent from a common ancestor that had the feature.

Hennig's seminal contribution (Hennig 1966) was to note that in a system evolving via descent with modification and splitting of lineages, characters that changed state along a particular lineage can serve to indicate the prior existence of that lineage, even after further splitting occurs. The "Hennig Principle" follows from this: homologous similarities among organisms come in two basic kinds, *synapomorphies* due to immediate shared ancestry (i.e., a common ancestor at a specific phylogenetic level), and *symplesiomorphies* due to more distant ancestry (Fig. 1). Only the former are useful for reconstructing the relative order of branching events in phylogeny—"special similarities" (synapomorphies) are the key to reconstructing truly natural relationships of organisms, rather than overall similarity (which is an incoherent mixture of synapomorphy, symplesiomorphy, and non-homology).

In the Hennigian system, individual hypotheses of putative homology are built up on a character-by-character basis, then a congruence test (using a *parsimony* principle) is applied to identify *homoplasies* (i.e., apparent homologies that are not congruent with the plurality of characters). One advantage of this approach is that it is applicable to all data types, ranging from traditional anatomical characters to alternative nucleotides at a homologous position in a DNA molecule (and phylogenies are best inferred from combinations of such diverse data types; Donoghue and Sanderson 1992; Mishler 1994). All that is required (in the phase of phylogenetic research commonly called "character analysis") is evidence for: (1) homology and heritability of a character across the taxa being studied, (2) independent evolution of different characters, and (3) presence in each character of a system of at least two discrete states.

Finally, classifications are applied to the resulting branching diagram (*cladogram*). A corollary of the Hennig Principle is that classification should reflect reconstructed branching order; only *monophyletic groups* should be formally named. A strictly monophyletic group is one that contains all and only descendents of a common ancestor; these are groups recognized by synapomorphies. A *para-*

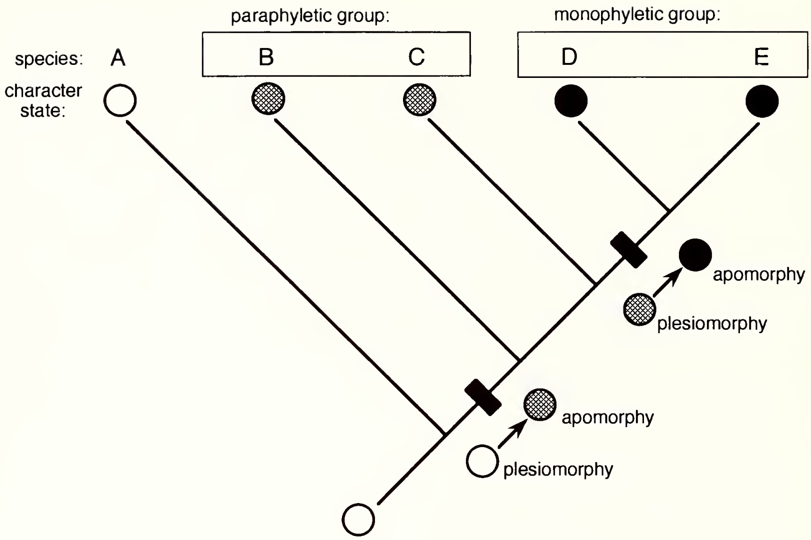

FIG. 1. A hypothetical cladogram illustrating definitions given in text. Shown is a phylogeny of five species (A–E) based on a number of characters. One character is mapped onto the cladogram; two evolutionary changes occurred in this character, giving it a three state transformation series (shown for generality as an open circle, partially-filled circle, and completely-filled circle—in reality this would be something like three different stamen numbers in the flower or three different nucleotides at one site in the DNA). These changes illustrate the relational nature of the distinction between plesiomorphy and apomorphy: initially, the partially-filled circle would represent the apomorphic state (relative to the open circle) at that branch of the phylogeny, but it would represent the plesiomorphic state at a later branch of the phylogeny (relative to the completely-filled circle). Two of the many possible higher-level groups are shown: a group D–E (supported by the synapomorphic final state in the transformation series) would be monophyletic, while a group B–C (supported by the symplesiomorphic intermediate state in the transformation series) would be paraphyletic.

phyletic group is one that excludes some of the descendents of the common ancestor; these are groups at best marked by symplesiomorphies. See Fig. 1 for the distinction between these two types of groups.

This elegant correspondence between synapomorphy, homology, and monophyly is the basis of the cladistic revolution in systematics. By restricting the use of the formal Linnaean system to hypothesized monophyletic groups, we can most efficiently summarize known data about attributes of organisms and also predict unknown attributes. For a recent example (from Systematics Agenda 2000, 1994), taxol (the drug used to control ovarian and breast cancer) was discovered in the bark of *Taxus brevifolia,* pacific yew. Three trees were needed for each patient, which was fatal for the trees at least, and could have lead to endangerment of the species. A random search for a source for taxol in other trees in the same environment would have taken years, but a search based on an understanding of phylogenetic relationships lead quickly to the European yew (*Taxus baccata*), which turned out to be a better source because the leaves could be used (a renewable resource).

Phylogenetic taxa are "natural" in the sense of being the result of the evolutionary process. Evolution by natural selection might under some extreme conditions cause organisms to become very similar in some respects even though they are unrelated. But such similarity will not be across the board, but rather in the suite of attributes being influenced by convergent selection (e.g., a hummingbird pollination syndrome, thorns, or succulence). Across the board, detailed similarity is more likely to be due to descent (homology; synapomorphy) than common environment (analogy). This is true for either morphological or molecular data; contrary to common perceptions, our recent, rapid progress in understanding relationships in plants is due less to the new sources of molecular data than it is to the new cladistic methods of analyzing data.

Phylogenetic criteria are necessary for the designation of taxa at the species level as well, although the details of applying the concepts of monophyly and apomorphy at that level are controversial and beyond the scope of this paper (see Mishler and Donoghue 1982; Mishler and Brandon 1987). The gist of the matter is that species taxa, like higher taxa, should be distinguished by distinct, apomorphic character states rather than by overall similarity. Thus traditional botanical concepts that view species as either clusters of similar plants or as sharing a common breeding system need to be reexamined, since these types of similarities are often plesiomorphic.

Phylogenetics and Conservation Biology

There is a widely perceived dichotomy between academic phylogenetic systematic studies and applied studies of floristics and plant conservation. This division has been aggravated by misunderstandings on both sides: academic researchers have been known to disdain concerns about utility of classifications, and resource managers have been known to complain about nomenclatorial changes resulting from improved taxonomic understanding. However, for efficient progress in the urgent business of plant conservation, it is important to recognize that practical issues such as identifying plants, making lists of species, and developing conservation plans *are* affected by the theoretical considerations discussed in the previous section. We don't want just *any* old name for these purposes, but rather a good name, one that reflects a natural phylogenetic entity. With natural

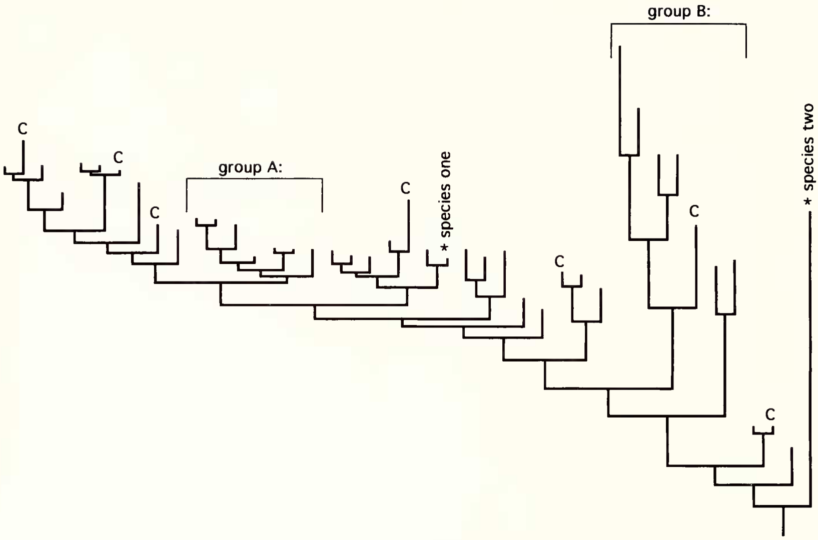

FIG. 2. A hypothetical cladogram illustrating the importance of phylogeny in setting conservation priorities. Shown is a phylogeny of 43 species; the branch lengths are proportional in the vertical direction to the number of evolutionary character changes along that branch. From the standpoint of preserving the maximum amount of phylogenetic diversity (and its closely associated genetic, morphological, physiological, and ecological diversity), species one would have a lower conservation priority than species two. Three groups of seven species each are also marked on the cladogram. By the same criterion, group A would have a lower conservation priority than group B. Group C, consisting of the same number of species scattered across the cladogram, would have a much higher conservation priority than either group A or B. In fact, group C would have a higher conservation priority than groups A and B *taken together.* Thus, the number of species in a locality is by itself a poor indicator of its priority for conservation (see text for further explanation).

taxa, one can rationally talk about issues such as evolution, biogeography, and extinction. With unnatural taxa (i.e., artificial assemblages of unrelated populations) such issues are meaningless, and conservation efforts are hampered at best (and misguided at worst). Without knowing the relationships of populations and species, there is no practical way to conserve them. We need to set priorities.

All species are not equal in a phylogenetic sense (or any other sense for that matter; e.g., Mishler and Donoghue 1982). As has been pointed out by a number of pioneering cladistic conservation biologists (Vane-Wright et al. 1991; Faith 1992a, 1992b), conservation priorities can best be set by a consideration of the phylogenetic relationships among species. This is because all attributes of organisms (genetic similarities, ecological roles, morphological specializations) tend strongly to be associated with phylogeny. As pointed out by David Wake (personal communication), from the standpoint of preserving the maximum phylogenetic diversity (and its associated attributes), saving a long-branch species (i.e., one such as the coast redwood or Santa Lucia fir with much change along the terminal branch, either due to extinction or rapid evolution) should carry a higher priority than saving a short-branch species (i.e., a goldenrod differing in only a few minor features from near relatives). Furthermore, saving a community of 100 species of diverse phylogenetic relationships should carry a higher priority than saving a community of 200 species belonging to only a few large genera (see Fig. 2 for an illustration of these points). Thus, systematic considerations should play a much more important role in conservation biology than they have to date (e.g., there are whole books devoted to the field that do not even mention this key role of phylogenetic systematics).

In an ideal world all species could be preserved—in this world of limited resources (time, money, and public goodwill) an index based on phylogeny must be developed to help us preserve the maximal genetic, morphological, chemical, and ecological diversity. The general public will be much more supportive of species preservation efforts that are carefully focused and justified in this way, rather than of uncritical, across-the-board efforts. Phylogeny reconstruction is thus not just an academic exercise, but rather the fundamental basis of a truly practical taxonomy.

Educational Needs

A major international planning effort has been taking place over the last three years to define a clear set of attainable goals in systematics. This effort is entitled *Systematics Agenda 2000,* one major component of which will be in the area of enhancing research centers for systematics (with their associated collections and databases); another of which will be in the area of education (training an expanded work force in a broad array of necessary skills). There are a number of productive and influential systematic research centers in California, yet only a small handful of universities have retained strong, broad-based systematics programs and are thus poised to respond to the current educational challenges. California's biodiversity is currently at great risk, and those few centers of research excellence in systematics that are also associated with first-class education programs have an especially important role to play.

Because of its unusual combination of attributes, with large herbaria and botanical garden as well as a number of supporting laboratories located within a major research university, UC Berkeley can make a unique contribution within California (and indeed the western United States) to these educational challenges. What, in particular, can the Jepson Herbarium contribute? One obvious area is in research, but since this area has always been a focus and is being addressed by other papers in this issue, I will emphasize another area that has not been a historical focus of the Jepson Herbarium: education.

General educational needs can be placed into six categories, as follows:

1. Ph.D. studies. The need to train specialists in systematics to "read" the biological information present in natural diversity has never been greater. Systematists must have a range of technical skills to extract information at all levels of inquiry (e.g., DNA sequences, organic chemistry, anatomy, morphology, ecology) and a broad theoretical background to interpret this information correctly. Modern biological systematics integrates a diverse array of disciplines ranging from molecular, cell, and developmental biology, to ecology, evolutionary biology, and philosophy. Data-gathering techniques are becoming increasingly diversified, complex, and numerical (even though field studies of ecology and distribution remain as important as ever). Specialists need to be trained in all groups of organisms, plants as well as the more popular animal groups, cryptogams as well as the more heavily studied flowering plant groups.

If graduate students are to integrate subjects, they have to be proficient in them. Accordingly, students of evolutionary processes and products all should obtain backgrounds in population biology, biogeography, paleontology, phylogenetics, and systematics. The identification of critical phylogenetic problems to apply new techniques to, and the integration of new data into an existing morphological framework, are only possible through such in-depth training in both the conceptual basis of systematics and the biology of some specific group of organisms. Attaining such breadth and depth requires a research university with a spectrum of faculty specialties; such a spectrum is represented in the biology departments at UC Berkeley, particularly in Integrative Biology and Plant Biology.

With the addition of several new faculty (myself, Bruce Baldwin, and a new systematic mycologist in the University and Jepson Herbaria; Nan Arens in the University Museum of Paleontology) to the existing faculty in plant systematics and evolution, we can provide an outstanding graduate program in this traditional emphasis of a research university. However, we must not forget other areas where we can make a contribution.

2. Postdoctoral studies. An important part of a complete education in a synthetic discipline such as systematics is a postdoctoral period of training. This appears to be the ideal time for a generally trained systematist to become familiar with a new technology to apply in their specialty. There is a two-way relationship between postdocs and an institution. The postdoc is benefited by working in a different intellectual environment, learning new techniques, and having a relatively unfettered period of time to complete and publish research before taking a professorial position. The institution benefits from having new Ph.D.s bring fresh ideas and expertise into its program, which is stimulating for both faculty and graduate students. We need to find the resources to make this a viable part of our program in plant systematics.

3. General training in systematics for other biologists. The recognition is dawning that an understanding of systematics is just as important as statistics or chemistry in the required background knowledge for all biologists, even those who will specialize in other areas such as medicine or biotechnology. Any biological study that compares two or more organisms, or even studies on a single organism that will eventually be consulted by biologists interested in other organisms, should incorporate some elements of systematics. Examples include the use of the systematic literature to intelligently select study systems, positive identification of study organisms by specialists (with application of correct nomenclature and deposition of voucher specimens in a permanent collection), and the use of appropriate concepts of taxa (especially at the species level) and formal comparative methods to determine the generality of study phenomena (e.g., Brooks and McLennan 1991). A phylogenetic tree produced from an analysis of the relationships of species constitutes a pattern of descent (common ancestry), modification (changes in ancestral characters), and spatial relationships (patterns of biogeography). In theory, all changes (anagenetic as well as cladogenetic) that occur during evolutionary descent can be incorporated into this tree. This allows investigators to assess the extent to which either recent or historical factors have influenced the relationships among groups or between the ecology and phylogeny of a single group. We intend to continue inserting such principles of systematics into the large Integrative Biology undergraduate major at UC Berkeley, as is being done in an increasing number of institutions across the state.

4. Professional training in areas such as curation, environmental assessment, and conservation biology. There is a growing need for professionals in these areas, requiring very different training than that necessary for the Ph.D. route. In fact, the specialization required these days for the latter route is such that Ph.D.'s are usually not well-equipped to carry out broad inventories. This distinction is not meant to denigrate either route, or to downplay the obvious connections between them detailed earlier; it is merely a recognition that the field is too big to comprehend all at once and that a division of labor is called for. The training needed to carry out a high-powered monographic and phylogenetic study of one group of plants is just different than the training needed to carry out a cutting-edge environmental inventory and conservation plan for many groups of plants.

Several campuses of the California State University system have traditionally had strong Master's programs in these areas, while UC Berkeley has not. We hope to rectify this gap here; I am looking into the feasibility of beginning a collaborative program in these areas, probably in connection with the UC Botanic Garden and the UC Extension program. The general idea would be to have students take a program of courses in systematics, ecology, and some environmental policy, with an intervening summer used for practical experience (e.g., an internship to learn about curation, environmental impact statements, field work, or specimen-based research). Such a program has the potential of being a model for the future; it should offer unique opportunities and thus be popular enough to be self-supporting. We are asking for feedback and assistance in setting this up in a maximally useful way.

5. Educational programs for interested amateurs. There is a great deal that can be (and has been) contributed by trained amateurs, in areas such as documenting precise geographic ranges of species, discovering new variants, and testing new uses for wild species in horticulture. To this end, we will use the resources of the Jepson Herbarium to offer courses in systematics. For example, the Weekend Workshops on systematics of specific problem groups, designed for both the professional botanist and the interested amateur, are our first attempts in this area. We hope this series will be the first of many general courses of this nature, and again would be glad to have feedback on how we could best serve your needs.

6. Educational programs for school children. Many youngsters (especially in the minority community from inner city schools) never have the chance to consider professional opportunities in organismal botany, because they get no exposure to these areas in school or at home. An understanding of the scientific study and importance of biodiversity should be an important part of the curriculum for all students. We plan to reach out to the local high schools first, partly because there are fewer of them than elementary schools, but also because this is a key age for career choice. Reaching out to the elementary schools would require the development of a docent program, and it may be that we can join forces with the already excellent programs for elementary school children put on by the UC Botanical Garden.

We, the staff, associates, and friends of the Jepson Herbarium, need to take advantage of the currently expanding concerns for the study and preservation of biodiversity among the public, and take a leadership role in the state of California and the United States in general. In doing so we must channel the public's rather unfocused concerns through educational efforts at all these levels. There is only a limited amount of time within which to save the diversity of native plants that remains in California. We need to concentrate on those areas in which a university-associated herbarium can make a unique contribution. We will continue the tradition of rigorous scientific *research,* augmented with new concepts and technologies. Furthermore, we will pursue innovative ways of organizing and presenting information about California plants. We will develop enhanced *education* programs, as detailed previously. And finally, we will relate and focus these research and education efforts on one of the most critical problems facing California today: the *conservation* of its diverse, beautiful, and useful flora.

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